Eur J Wildl Res (2013) 59:237–243
DOI 10.1007/s10344-012-0671-x

ORIGINAL PAPER

Overestimates of maternity and population growth rates in multi-annual breeders

Guillaume Chapron · Robert Wielgus · Amaury Lambert

Received: 10 February 2012 / Revised: 8 August 2012 / Accepted: 27 September 2012 / Published online: 11 October 2012

Abstract There has been limited attention to estimating maternity rate because it appears to be relatively simple. However, when used for multi-annual breeder species, such as the largest carnivores, the most common estimators introduce an upward bias by excluding unproductive females. Using a simulated dataset based on published data, we compare the accuracy of maternity estimates derived from standard methods against estimates derived from an alternative method. We show that standard methods overestimate maternity rates in the presence of unsuccessful pregnancies. Importantly, population growth rates derived from a matrix model parameterized with the biased estimates may indicate increasing populations although the populations are stable or even declining. We recommend the abandonment of the biased standard methods and to instead use the unbiased alternative method for population projections and assessments of population viability.

Keywords Maternity rate · Bias · Grizzly bear · *Ursus arctos* · Growth rate

Communicated by M. Artois

Electronic supplementary material The online version of this article (doi:10.1007/s10344-012-0671-x) contains supplementary material, which is available to authorized users.

G. Chapron (✉)
Grimsö Wildlife Research Station, Department of Ecology,
Swedish University of Agricultural Sciences,
73091 Riddarhyttan, Sweden
e-mail: gchapron@carnivoreconservation.org

G. Chapron
Conservation Biology Division, Institute of Ecology and
Evolution, University of Bern,
Baltzerstrasse 6,
CH–3012 Bern, Switzerland

R. Wielgus
Département Ecologie et Gestion de la Biodiversité,
Museum National d'Histoire Naturelle,
57 rue Cuvier,
75231 Paris Cedex 05, France

R. Wielgus
Large Carnivore Conservation Laboratory, Department of Natural
Resource Sciences, Washington State University,
Pullman, WA 99164-6410, USA

A. Lambert
Laboratoire de Probabilités et Modèles Aléatoires,
UPMC Université Paris,
06, Case courrier 188, 4, Place Jussieu,
75252 Paris Cedex 05, France

Introduction

Improving management recommendations from population models is dependent upon parameterizing them with all available information in an unbiased way. For simple matrix and stage-structured population models, at least two kinds of demographic parameters are needed: survival and maternity rates. Estimating survival has been the focus of extensive research and can be done following well-established methods (Thomson et al. 2008; Williams et al. 2002). Estimating maternity rate appears to be simpler and does not require a careful attention because accurate and unbiased estimates of maternity rate *Mx* (i.e., the average number of offspring this year for each of the mothers this year) are relatively easily obtained for annual breeders: one simply censuses the number of offspring (*No*) and females (*Nf*), and the resulting ratio (*No*/*Nf*) provides the maternity rate for that year (Akçakaya et al. 1999). This method is, however, inadequate for multi-annual breeders with extended birth intervals such as the largest carnivores. Three methods that were described in the study of McLellan (1989) for grizzly bears (*Ursus arctos horribilis*) are generally used. In Method 1

(M1), reproductive rate equalled to "the total number of cubs observed divided by the total number of bear years required to produce them". In Method 2 (M2), the reproductive rate equalled to "the average of each individual's rate". In Method 3 (M3), the reproductive rate equalled to the "average litter size divided by the average interbirth interval". The author added that M1 and M2 included "information only from female bears that were radio-tracked through at least one interbirth interval", and on the contrary, more information was available for estimating the reproductive rate using M3 because "all litter size data could be used". An improvement of M3 appeared later in the study of Eberhardt et al. (1994) and Hovey and McLellan (1996) who developed bootstrapped estimates for *Mx* and associated 95 % confidence intervals for grizzly bears, using mean litter size divided by mean birth interval ratio with individual litters and birth intervals as sample units. Nevertheless, the original M3 remains the most widely used and standard method to estimate reproductive rate not only for grizzly bears but also for other large carnivores such as leopards, mountain lions, or tigers (Boyce et al. 2001; Eberhardt et al. 1994; Karanth and Stith 1999; Logan and Sweanor 2001; Mace and Waller 1998; McLellan 1989; McLoughlin et al. 2003a; Miller 1997; Pease and Mattson 1999; Schwartz et al. 2003; Wakkinen and Kasworm 2004; Wielgus 2002; Wielgus and Bunnell 1994, 2000; Wielgus et al. 1994; Kerley et al. 2003; Owen et al. 2010).

The problem with using these three methods is the potential for biasing estimates of *Mx* upwards, hence overestimating population growth and viability. It can be intuitively understood that no observation of newborns (afterwards termed "litter sizes of zero") will not readily be included in calculating mean litter size. It can be equally understood that birth intervals (e.g., number of years between successive, successful births) must be closed to calculate mean birth interval, i.e., each individual needs at least two reproductive events to have a complete interval. Hence, litter sizes of zero and indeterminate or open-ended birth intervals are excluded in methods M1, M2, and M3. This potential bias could be particularly severe in unproductive populations where females commonly fail to produce a litter or have birth intervals longer than the period of study. These unproductive animals would be excluded, yielding an upwardly biased estimate of *Mx*. Hovey and McLellan (1996) recognized this problem of a potential bias but believed it was unimportant in their grizzly bear study because only four of 14 females with observed litters failed to provide a closed interval. However, it should be mentioned that only 60 % (14 of 23) adult females were observed to produce litters in their study.

Further studies have tried to address the bias potentially introduced using methods M1, M2, and M3. Some researchers (Lambert et al. 2006) modified the standard mean litter size/mean birth interval ratio by estimating percentage of unproductive females (those with litters of zero and indeterminate birth intervals) and multiplying the reciprocal of this percentage by the standard ratio estimate. Others (Chapron et al. 2003; McLoughlin et al. 2003b; Wielgus et al. 2001) estimated *Mx* using a probabilistic approach—which incorporates the probabilities of producing from 0 to *N* offspring on an annual basis. Schwartz and White (2008) recognized the bias of McLellan (1989) methods and proposed a completely different approach through computing transition probabilities between female states defined as female alone, with cubs, yearlings, or 2-year olds. Garshelis et al. (2005) mentioned the potential bias in the standard method (only 13 birth intervals were closed compared to 23 open-ended intervals in their study), and they calculated *Mx* by proposing an alternative method (labeled M4) which is to divide each year the number of offspring by the number of females and then to compute the arithmetic mean over years. They found that their estimate of grizzly bear *Mx* was also among the lowest ever recorded and attributed that to some combination of real biological differences and/or biased overestimates in other studies.

If these four different methods used to parameterize population models do not give the same results, then some conservation assessments and management strategies may be hazardous while appearing safe if *Mx* is biased upwards. Are some populations of multi-annual breeders previously estimated to be growing using the standard method M3 actually declining? Is the alternative method M4 always accurate? How large is the bias in the standard method M3 and should all analyses and recommendations based on that method be reassessed using the alternative method M4? In this paper, we compare McLellan (1989) M1, M2, and mostly M3 computations of reproductive rates for multi-annual breeders against the alternative method M4 to estimate maternity rate *Mx* using simulated data and taking the grizzly bear as an illustrative example. We compare the outcomes of each method and how they are affected by sampling duration (years of monitoring), sample size (number of females), and population parameters. We also compare how method M3 of estimating *Mx* affects modeled population growth rates and provide a theoretical quantification of the bias introduced by method M3.

Methods

Illustrative example

We first consider an illustrative example based on a representative grizzly bear dataset (Table 1) to allow one to understand how methods M1, M2, M3, and M4

Table 1 Illustrative life history dataset giving the reproductive status for 12 grizzly bear females during 6 years

	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
F_1	–	3[a]	3	3	0	0
F_2	2[a]	*2*	*2*	*2*[a]	0	0
F_3	0	0	2[a]	2	2	0
F_4	3[a]	3	3	3	–	–
F_5	–	1[a]	*1*	*1*	*1*[a]	1
F_6	2[a]	*2*	*2*[a]	2	2	2
F_7	4[a]	*4*	*4*	*4*	*2*[a]	–
F_8	0	0	0	0	2[a]	0
F_9	–	2[a]	*2*	*2*	*3*[a]	3
F_{10}	0	0	0	0	0	–
F_{11}	–	–	0	0	0	0
F_{12}	2[a]	0	0	0	–	–

Values show the numbers of cubs following a female. Zeros are unsuccessful pregnancies, and en dashes are females that were not followed this year (not yet marked or had left the sample). For each female, items set in italics indicate a closed interbirth interval. Methods M1 and M2 consider interbirth intervals as the duration required to produce a litter; hence, their calculations include only litters at the end of closed interbirth intervals

[a] Newborn litters

differ. Based on the second author knowledge of bear biology, we generate a dataset with 12 adult females studied over 6 years (a typical graduate student or agency project on large carnivores). Females in this example give birth to one to four cubs every 2–4 years, as is the accepted norm for most grizzly bear populations (Schwartz et al. 2003). Environmental stochasticity is built into the dataset with good and bad years (e.g., year 1=good, year 6=bad) to reflect typical booms and busts centered on bear foods such as berry crops, salmon, and ungulate prey (Wielgus 2002).

With method M1, one computes the sum of all litters resulting from a closed interbirth interval (those litters are italics and marked by "a" in Table 1) and divide it by the sum of all closed interbirth interval durations (shown in italics in Table 1). For the illustrative dataset, the M1 method returns Mx=(2+1+2+2+3)/(3+3+2+4+3)=0.67 cubs/female/year. Note that an interbirth interval is seen as "how long it has required to produce a litter since the last one" in agreement with McLellan (1989), and, therefore, we count for each interval only the litter at the end of the interval and not the one at the beginning.

With method M2, one computes a maternity rate for each female by dividing the sum of their litter sizes (at the end of closed interbirth intervals—like M1) by the sum of their closed interbirth interval durations and then computes the arithmetic means of these individual rates. For the illustrative dataset, the M2 method returns: Mx=(2/3+1/3+2/2+2/4+3/3)/5=0.7 cubs/female/year.

With method M3, one divides the average litter size by the average closed interbirth interval duration. For the illustrative dataset, the M3 method gives an average litter size of (3+2+2+2+3+1+1+2+2+4+2+2+2+3+2)/15=2.2 and an average interbirth interval of (3+3+2+4+3)/5=3 and returns Mx=2.2/3=0.73 cubs/female/year.

With the alternative method M4, one first computes an average maternity rate for each year, dividing the total number of cubs this year by the total number of monitored females, and then computes the arithmetic mean of these yearly rates. For the illustrative dataset, the M4 method returns Mx=(13/8+6/11+4/12+2/12+8/10+0/8)/6=0.58 cubs/female/year.

In this illustrative example, an obvious major drawback of methods M1, M2, and M3 is that they ignore females with interbirth intervals longer than the monitoring duration. As a consequence, seven females (#1, #3, #4, #8, #10, #11, and #12) are not included, and the Mx estimate uses only data from five of the 12 females in our sample—similar to the proportions (1/2) reported by Hovey and McLellan (1996) and (1/3) Garshelis et al. (2005). As precised by McLellan (1989), the standard method M3 uses more data, because all litter size data could be used to compute mean litter size; however, seven females are still excluded to compute mean interbirth interval. This comparison shows that the Mx estimates with M1, M2, or M3 are much larger (0.67–0.73) than with M4 (0.58) simply because of the bias of excluding open-ended intervals.

Simulated datasets

We then simulate life history datasets using a grizzly bear stochastic individual-based model parameterized with known demographic parameters and calculate Mx estimates using M1, M2, M3, and the alternative M4 methods. This approach, commonly termed recovering parameters from simulated data, allows us to check the accuracy of these different methods because the true value of maternity rate is known and can be calculated based on model parameters (see Section 1 in Supplementary Material).

We simulate the fate of a given number of female grizzly bears. Females give birth to litter whose size is drawn from a tabulated distribution, giving the specific probability q_n of having n=0 to three cubs. Unsuccessful females (those with zero cubs) return in estrus and attempt to give birth again the year after. Successfully breeding females raise their cubs and do not breed again until either all the cubs have died before reaching age of 3 years or have naturally dispersed when reaching age of 3 years. We run our model for both a productive, unhunted population and an unproductive, hunted population. Parameters, such as age-specific survival

probabilities, are obtained from the Selkirk grizzly bear population for the unhunted case and from the Kananaskis grizzly bear population for the hunted case (see Section 2 in Supplementary Material). Starting from a population consisting of females with random numbers of cubs, the model runs for a number of time steps corresponding to the study duration and records litter size over years for all the simulated females, and this process is iterated 10,000 times. For both unhunted and hunted populations, we use the model to generate life history datasets, from one to 10 radio-tracked females from 1 to 10 years. The program estimates maternity rates using methods M1, M2, M3, and the M4 alternative. Using values of q_n and survival rates from the unhunted and hunted populations, we compare the exact value of *Mx* (see Section 1 in Supplementary Material) with estimates obtained by the four methods applied to our simulated dataset.

We then use an age-structured female Leslie matrix model (Caswell 2001) to analyze how asymptotic growth rate λ would be affected by biased estimates of *Mx*. For both unhunted and hunted population consisting of 10 females, we calculate the mean of *Mx* estimated by method M3 from the simulated data and obtain growth rate as the largest real eigenvalue of the Leslie matrix. Finally, we examine how the probability of unsuccessful pregnancy q_0 may affect the bias on estimates of *Mx* using method M3 (see Section 4 in Supplementary Material).

Results

We find similar inconsistent results between methods M1, M2, and M3 and the M4 alternative. Method M4 returns on average the exact same value as the one computed directly from model parameters (unhunted: *Mx*=0.72, hunted: *Mx*=0.49).

For the simulated unhunted population (Fig. 1), the value of *Mx* computed from the alternative method M4 is consistent across numbers of monitoring years and numbers of monitored females at *Mx*=0.72 (SD varying according to sampling

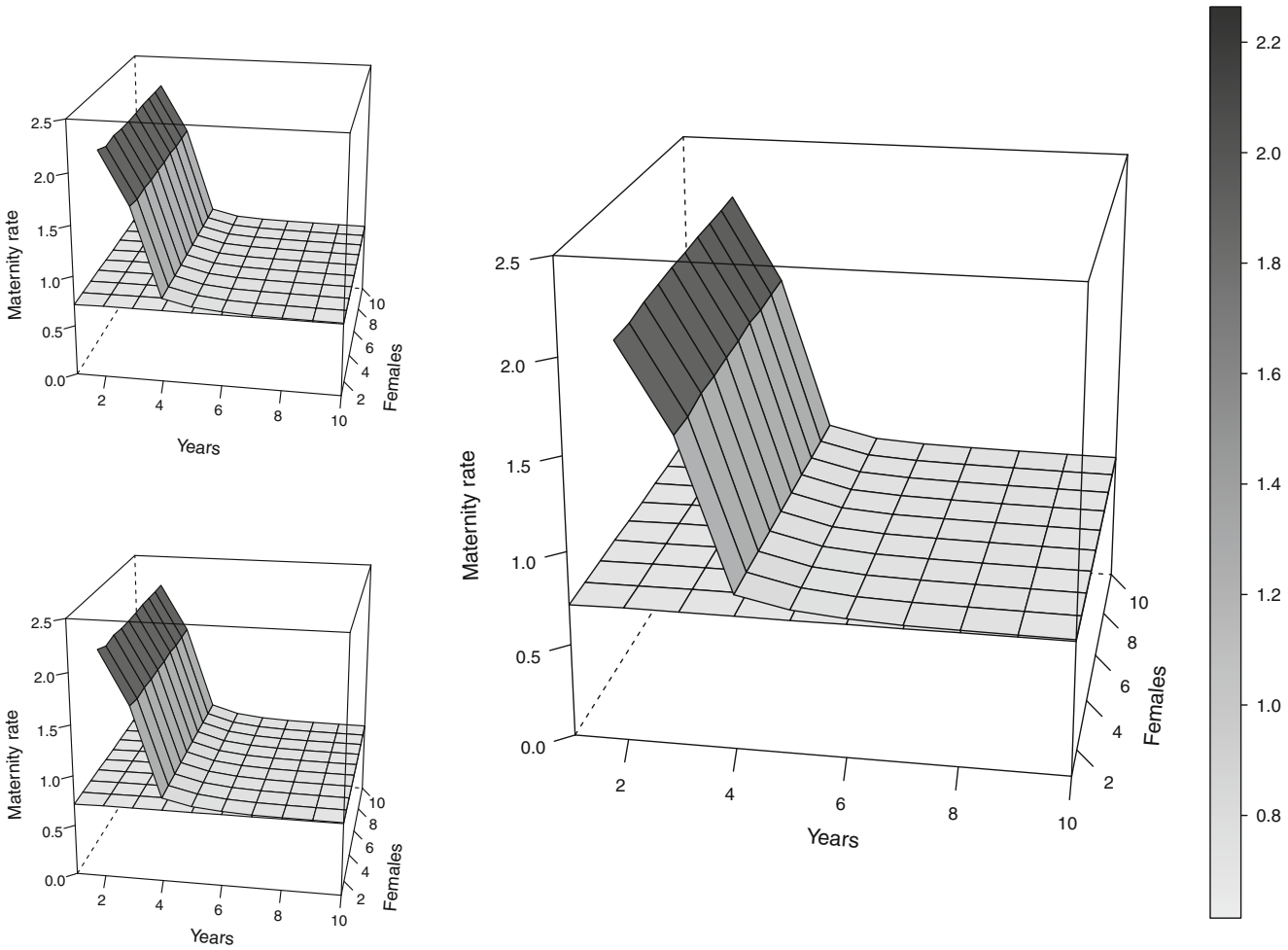

Fig. 1 Maternity rate *Mx* averaged estimates with simulated data for an unhunted population as a function of numbers of monitored years and females. Unit for maternity rate and on the gray scale is in cubs/female/year. M1 *top left*, M2 *bottom left*, M3 *right*, M4 *is the flat surface* shown on all figures. Note that methods M1, M2, and M3 cannot be used for study duration of 1 year. The exact correct value is *Mx*=0.72 cubs/female/year

duration and sample size). By contrast, methods M1, M2, and M3 are upward-biased and duration-dependent. With method M3, a grizzly bear population of 10 females would, on average, have an *Mx* estimate of 1.69±0.53 if population was monitored during 3 years, 0.82±0.24 if population was monitored during 4 years, and 0.75±0.08 if population was monitored during 5 years. Varying the sample size of monitored females does not affect the bias introduced by methods M1, M2, and M3.

For the simulated hunted population, the bias is worse (Fig. 2). The value of *Mx* computed from the alternative method M4 is consistent across numbers of monitoring years and monitored females at *Mx*=0.49 (SD varying according to sampling duration and sample size). By contrast, methods M1, M2, and M3 are upward-biased and duration-dependent. With method M3, a grizzly bear population of 10 females would, on average, have an *Mx* estimate of 1.20±0.31 if population was monitored during 3 years, 0.66±0.20 if population was monitored during 4 years, and 0.57±0.09 if population was monitored during 5 years. Varying the sample size of monitored females does not affect the bias introduced by methods M1, M2, and M3.

As a consequence of the upward bias in *Mx*, the standard method M3 overestimates population growth (Fig. 3). For the unhunted population monitored 3 years, method M3 returns a growing population (λ=1.143), but the unbiased M4 method returns a much lower growth rate (λ=1.049) and matches the true population growth rate. For the hunted population monitored over 3 years, method M3 returns a growing population (λ=1.097), but the unbiased M4 method indicates the population is stable (λ=1.008) and matches the true population growth rate.

The bias in *Mx* using the standard M3 method increases with probability of unsuccessful pregnancies q_0. For either the unhunted or hunted population, the bias is nonexistent when this probability is 0, but reaches +10 % for q_0=0.23, +25 % for q_0=0.43, and +50 % for q_0=0.6 (hunted case on Fig. 4). For extremely unproductive populations (q_0=0.8), method M3 overestimates *Mx* by 136 %.

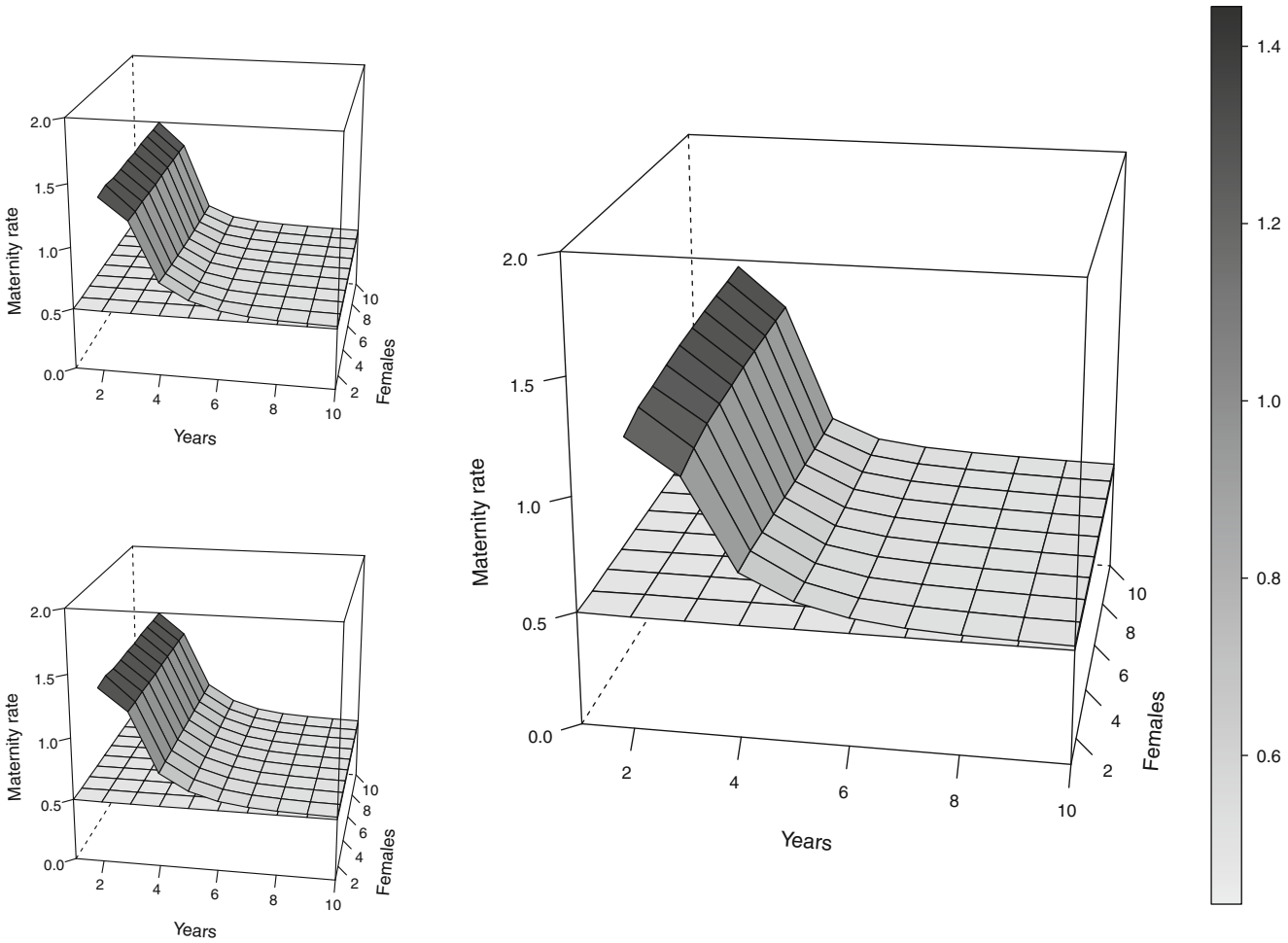

Fig. 2 Maternity rate *Mx* averaged estimates with simulated data for a hunted population as a function of numbers of monitored years and females. Unit for maternity rate and on the gray scale is in cubs/female/year. M1 *top left*, M2 *bottom left*, M3 *right*, M4 *is the flat surface* shown on all figures. Note that methods M1, M2, and M3 cannot be used for study duration of 1 year. The exact correct value is *Mx*=0.49 cubs/female/year

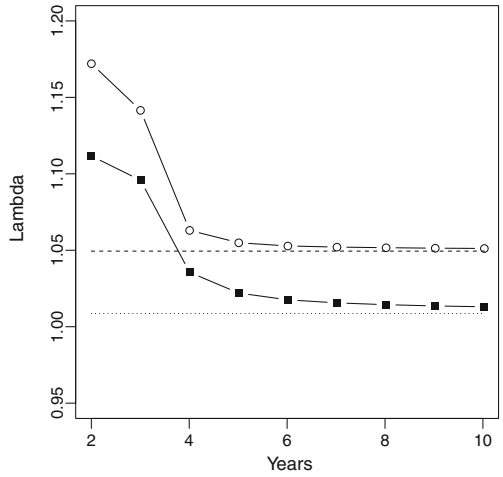

Fig. 3 Estimate of λ when using *Mx* computed by method M3 with simulated data for hunted (*black squares*) and unhunted (*empty circles*) populations with 10 females as a function of monitoring duration. Population growth rate λ computed with exact method M4 is 1.049 (unhunted population, *dashed line*) and 1.008 (hunted population, *dotted line*)

Discussion

Our results indicates that methods M1, M2, and M3 yield overestimated, inconsistent, and duration-dependent estimates of *Mx*. Increasing the sampling duration to about 7–8 years would lower the bias. To completely eliminate the bias, all females in the sample would need to produce young, and the sampling duration would need to last an infinite number of years, which are both unrealistic. Increasing the sample size of monitored females does not decrease the bias. We agree that low precision is an important problem for low sample sizes; however, our point here is to show that even by considering that all individuals in a population could be observed, methods M1, M2, and M3 would still not return the correct value of maternity rate. We show that the bias from using the M3 standard method is a continuously growing function of the probability of unsuccessful pregnancies, and this method can therefore not detect a reduction of maternity rate due to an increase of unsuccessful pregnancies. By contrast, the M4 alternative yields unbiased estimates of *Mx* regardless of numbers of monitored females and duration of monitoring. In particular, method M4 does not introduce bias for data collected over short periods because it is not dependent on the existence of closed interbirth intervals; even though precision at small sample size will be an issue (e.g., (Devenish Nelson et al. 2010)).

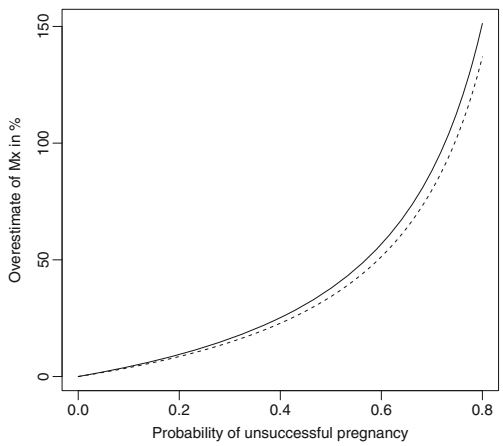

Fig. 4 Overestimate *b* of *Mx* computed from its analytical expression derived in the Methods Section, when using the M3 method (hunted population – *continuous line*, unhunted population – *dashed line*), as a function of probability of unsuccessful pregnancy q_0

The bias is greater in the unproductive, hunted populations than in the productive, unhunted population for two reasons. First, the hunted population has a higher percentage of unproductive (no cubs) estrous females per year (20 vs. 12 %) and these "zero" females would be excluded in the method M3. Second, the hunted population has a smaller mean litter size, which has a higher probability of disappearing. Loss of a litter then results in more females moving to the estrous condition, and estrous females have a higher probability of being a "zero" in the unproductive population.

We report estimates of *Mx* for each method as average values from 10,000 simulated datasets. Because our demographic model is stochastic, it introduces a random variability in the data simulation process. For example, while averaged M4 estimates are a flat surface equal in all points to the correct value of *Mx* on Figs. 1 and 2, each individual M4 estimate from a single dataset may not necessarily be equal to the correct value—also the case for dataset obtained in real field conditions. However, this should not suggest an inaccuracy of method M4. As shown in Section 4 of the Supplementary Material, the density distribution of *Mx* estimates from method M4 is symmetrical and centered around the correct value (contrary to estimates from methods M1, M2, and M3), which reveals that the variation in *Mx* estimates from method M4 is not caused by any overestimating bias but simply by the stochasticity in the data.

These simulated results are consistent with the empirical data reported by Garshelis et al. (2005). They used the unbiased M4 method and reported an unexpectedly low *Mx* compared to other North American grizzly bear populations (0.24 vs. 0.32). They attributed their relatively low value of *Mx* due to some combination of real biological differences and/or bias in the other studies. We concur with Garshelis et al. (2005) that they found an unexpectedly small *Mx* and that the differences in estimated *Mx* were substantial—but the evidence presented here suggests that the main cause may be bias in other studies using the biased method M3 (Eberhardt et al. 1994; Hovey and McLellan 1996; Miller 1997), not an abnormally small *Mx* in their study area. We suspect that estimates of *Mx* reported in the literature using method M3, including our own previous work (Wielgus et al. 1994), may be biased overestimates. Despite a low elasticity of λ to *Mx* (Wielgus

et al. 2001), the bias was large enough to overestimate λ and have a stable, or even moderately declining, population considered as a growing one.

These results suggest that previous reports of high population growth, λ=1.08 (Hovey and McLellan 1996), λ=1.07 (Eberhardt et al. 1994), may be due to use of the biased estimates of *Mx* and not real gains in population numbers. For example, Wielgus and Bunnell (1994) and Wakkinen and Kasworm (2004) reported that the threatened Selkirk Mountain grizzly bears were stable and/or increasing, but both used the biased method M3. The results of the present paper suggest that the threatened Selkirk population may not be increasing towards recovery, but may be in fact, only stable or declining. The same conclusion may apply to the threatened Yaak population (Wakkinen and Kasworm 2004)—it may be declining much more rapidly than previously reported. Our results should incline researchers to abandon the use of the biased standard method M3 for species characterized by extended parental care and instead to use the unbiased method M4 for population projections and assessments of population viability.

Acknowledgments Funding and support was provided by the Centre National de la Recherche Scientifique Laboratoire d'Ecologie; Museum National d'Histoire Naturelle Département Ecologie et Gestion de la Biodiversité; National Science Foundation; US Department of Energy, Bonneville Power Administration, Fish and Wildlife Program; Université d'Angers; Université Pierre et Marie Curie; Swedish University of Agricultural Sciences; and Washington State University.

References

Akçakaya HR, Burgman MA, Ginzburg LR (1999) Applied population ecology: principles and computer exercises using RAMAS EcoLab 2.0. Sinauer Associates, Sunderland

Boyce MS, Blanchard BM, Knight RR, Servheen C (2001) Population viability for grizzly bears: a critical review. International Association for Bear Research and Management - Monograph Series 4

Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland

Chapron G, Quenette PY, Legendre S, Clobert J (2003) Which future for the French Pyrenean brown bear (*Ursus arctos*) population? An approach using stage-structured deterministic and stochastic models. Comptes Rendus - Biologies 326(suppl 1):S174–S182

Devenish Nelson ES, Harris S, Soulsbury CD, Richards SA, Stephens PA (2010) Uncertainty in population growth rates: determining confidence intervals from point estimates of parameters. PLoS One 5(10):e13628. doi:10.1371/journal.pone.0013628

Eberhardt LL, Blanchard BM, Knight RR (1994) Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Can J Zool 72(2):360–363

Garshelis DL, Gibeau ML, Herrero S (2005) Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. J Wildl Manag 69(1):277–297

Hovey FW, McLellan BN (1996) Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Can J Zool 74 (8):1409–1416

Karanth UK, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Christie S, Jackson P (eds) Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp 110–113

Kerley LL, Goodrich JM, Miquelle DG, Smirnov EN, Quigley HB, Hornocker MG (2003) Reproductive parameters of wild female Amur (Siberian) tigers (Panthera tigris altaica). J Mammal 84 (1):288–298

Lambert CMS, Wielgus RB, Robinson HS, Katnik DD, Cruickshank HS, Clarke R, Almack J (2006) Cougar population dynamics and viability in the Pacific Northwest. J Wildl Manag 70(1):246–254

Logan KA, Sweanor LL (2001) Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, California

Mace RD, Waller JS (1998) Demography and population trend of grizzly bears in the Swan Mountains, Montana. Conserv Biol 12 (5):1005–1016

McLellan BN (1989) Dynamics of a grizzly bear population during a period of industrial resource extraction. III. Natality and rate of increase. Can J Zool 67(8):1865–1868

McLoughlin PD, Taylor MK, Cluff HD, Gau RJ, Mulders R, Case RL, Boutin S, Messier F (2003a) Demography of barren-ground grizzly bears. Can J Zool 81(2):294–301

McLoughlin PD, Taylor MK, Cluff HD, Gau RJ, Mulders R, Case RL, Messier F (2003b) Population viability of barren-ground grizzly bears in Nunavut and the Northwest Territories. Arctic 56(2):185–190

Miller SD (1997) Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Federal Aid in Wildlife Restoration, Research Final Report, Study 4.26, June 1997

Owen C, Niemann S, Slotow R (2010) Copulatory parameters and reproductive success of wild leopards in South Africa. J Mammal 91(5):1178–1187

Pease CM, Mattson DJ (1999) Demography of the Yellowstone grizzly bears. Ecology 80(3):957–975

Schwartz CC, White GC (2008) Estimating reproductive rates for female bears: proportions versus transition probabilities. Ursus 19(1):1–12

Schwartz CC, Keating KA, Reynolds Iii HV, Barnes VG Jr, Sellers RA, Swenson JE, Miller SD, McLellan BN, Keay J, McCann R, Gibeau M, Wakkinen WF, Mace RD, Kasworm W, Smith R, Herrero S (2003) Reproductive maturation and senescence in the female brown bear. Ursus 14(2):109–119

Thomson DL, Cooch EG, Conroy MJ (2008) Modeling demographic processes in marked populations. Springer, New York

Wakkinen WL, Kasworm WF (2004) Demographics and population trends of grizzly bears in the Cabinet-Yaak and Selkirk ecosystems of British Columbia, Idaho, Montana, and Washington. Ursus 15(1):65–75

Wielgus RB (2002) Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biol Conserv 106(3):381–388

Wielgus RB, Bunnell FL (1994) Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. Biol Conserv 67(2):161–166

Wielgus RB, Bunnell FL (2000) Possible negative effects of adult male mortality on female grizzly bear reproduction. Biol Conserv 93 (2):145–154

Wielgus RB, Bunnell FL, Wakkinen WL, Zager PE (1994) Population dynamics of Selkirk Mountain grizzly bears. J Wildl Manag 58 (2):266–272

Wielgus RB, Sarrazin F, Ferriere R, Clobert J (2001) Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biol Conserv 98(3):293–303

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations: modeling, estimation, and decision making. Academic, San Diego